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Population Organization of Wild Pig-tailed Macaques (*Macaca nemestrina nemestrina*) in West Sumatra

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ABSTRACT. A field study on wild pig-tailed macaques was conducted in West Sumatra, Indonesia, during three periods from January 1985 to February 1987. During the nine months of the first two periods, unprovisioned monkeys were traced and observed. During the eight months of the last period, monkeys were provisioned and observed mainly at baiting sites. Three troops and ten solitary males appeared at the two baiting sites. Some males immigrated into and emigrated from the troops. The troops had a multi-male multi-female composition. The size of the various troops was 74, 49, and 81 individuals, respectively, and the mean adult sex ratio in the troops was 1:6.3; that is, markedly biased towards females. The home ranges of two of the troops overlapped considerably. When the troops encountered each other at the baiting sites, a clear dominance relationship was recognized. The troops differed in their integration as ranging units: two of the troops did not form subgroups (temporary fission and fusion of each troop), while the other troop frequently split into subgroups. Recent field studies on pig-tailed macaques have suggested a multi-leveled society with harem-type unit groups. However, in the present study, the troops observed had neither a substructure similar to harem-type groups nor a superstructure that emerged as a result of fusion of the troops. The unit group of the pig-tailed macaques appears to be a multi-male, matrilineal group.

Key Words: *Macaca nemestrina nemestrina*; Sex ratio; Subgrouping; Troop encounter; Intraspecies variation.

INTRODUCTION

Due to the furtive behavior of pig-tailed macaques (*Macaca nemestrina nemestrina*) and their elusiveness in their natural habitat, the ecology and social behavior of these monkeys have been difficult to analyze based on field studies (BERNSTEIN, 1967; CALDECOTT, 1986; ROBERTSON, 1986). BERNSTEIN (1967) observed groups which had a multi-male and multi-female composition, as well as solitary males, at Lima Belas, Malaysia, and such multi-male groups appeared to him to represent stable foraging and reproductive units. In contrast, CALDECOTT (1986) suggested that pig-tailed macaques (pigtails) had a fluid, multi-leveled society with "super-groups," "groups," "sub-groups," and solitary males. The "group" had a multi-male configuration: it temporarily split into "sub-groups" and temporarily fused into a "super-group." CALDECOTT also mentioned that such grouping tendencies "may be explicable in terms of aggregation and separation of one-male harem units with permanent female membership," although he deliberately avoided proposing this possible explanation as a definitive conclusion. ROBERTSON (1986), who conducted field studies in the Alas Valley, northern Sumatra, concluded that pigtails had "a society which contained three or more hierarchically organized grouping levels." The term "level" implied "bands" defined as a bisexual group whose members shared the same home range center, "sub-groups" composed of one or more adult females and their offspring, which associated in "bands" and "mixedbands" in which neighboring "bands" or some of their component units were associated. Furthermore, based on the observation that "bands" which contained two or three breeding males frequently split into "sub-groups" which contained only one breeding male, he proposed that the "band" may have been sub-structured into harems or polygynous one-male groups. However, because of the fragmental nature of the above observations without individual identifications in the tropical forest, the hypotheses put forward should be reconsidered on the basis of more detailed investigations.

After observing wild, unprovisioned pigtails for about nine months, I provisioned and observed the animals for about eight months. At the baiting sites, I collected detailed information on the social relationships based on individual identifications which were difficult to make during observations in the forest. The aim of the present report is to clarify the configuration of the unit group [as defined by ITANI (1977)] of this species and its social organization, from an analysis of the roll books of individuals who visited the baiting sites, of the movements of groups in the forest, and of the social interactions among the groups.

STUDY AREA

The study area is situated at the northern foot of Mt. Kerinci (3,805 m above sea level),

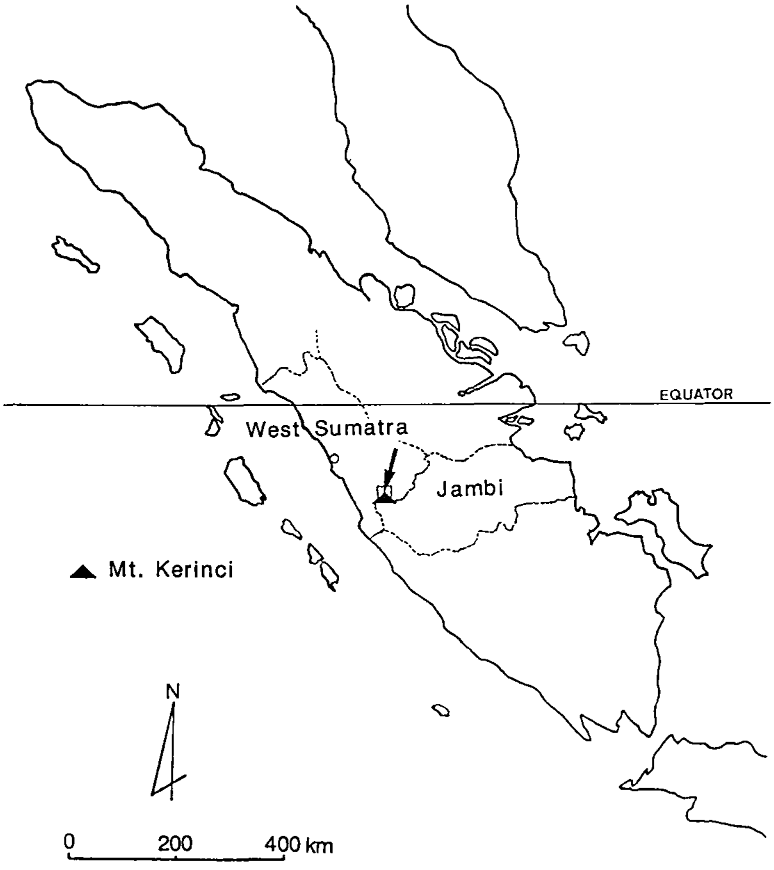

Fig. 1. Location of the study area, indicated by the arrow.

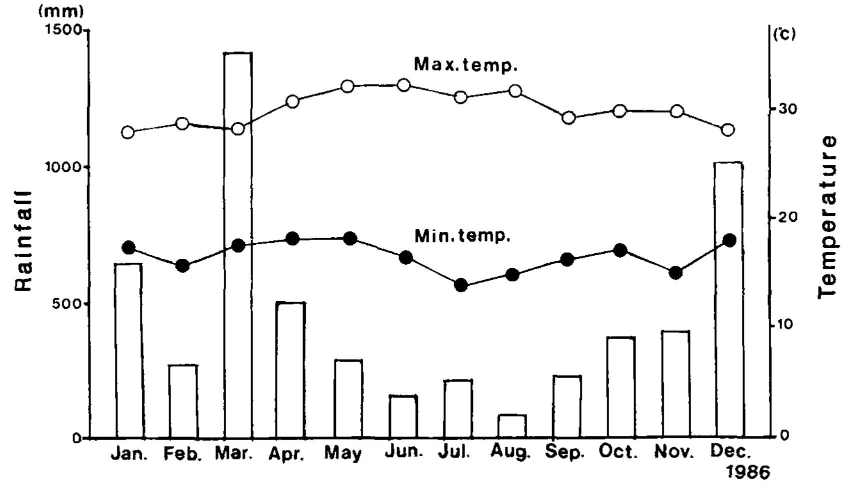

Fig. 2. Monthly rainfall and temperature in the study area in 1986. For rainfall, the histogram bars are monthly totals, and for temperature, circles are monthly maximum and minimum.

West Sumatra Province, Indonesia (1°36′S, 101°16′E) (Fig. 1). The altitude of the area ranges from 850 to 1,000 m above sea level. Most of the area is gently undulating or flat. The gradient ranges from 3% to 7% (DIT AGRARIA PROP SUMBAR, 1970). The annual rainfall at the study site was 5,570 mm in 1986. The rainfall varied seasonally: there were two periods of relatively high rainfall (March–May and October–January) and two periods of low rainfall (February and June–September). However, the monthly maximal and minimal temperatures did not show any such remarkable change (Fig. 2).

The floristic zone of this area corresponded to an ecotone between hill dipterocarp forest and upper dipterocarp forest (WHITMORE, 1984). However, the original vegetation in this area had been significantly disturbed by the establishment of tea (*Thea sinensis*) and coffee (*Coffea* sp.) plantations by the Dutch during the period from 1927 to 1941. Due to the abandoned tea plantations, and lumbering by the selective cutting method, the present vegetation can be said to be a mosaic of primary and secondary vegetation (Fig. 3). The secondary vegetation was typified by species such as *Melasotoma* sp., *Trema orientalis*, *Villebrunea rubescens*, *Mallotus paniculatos* etc., giant herbs such as wild gingers (Zingiberaceae), bananas (*Musa* sp.) and *Euphatorium inulifolium*, and giant woody climbers such as rattans (*Calamus caesius*).

Six primate species inhabited the area: pig-tailed macaques (*Macaca nemestrina*), crab-eating macaques (*Macaca fascicularis*), siamangs (*Hylobates syndactylus*), agile gibbons (*Hylobates agilis*), banded langurs (*Presbytis melalophos*), and slow loris (*Nycticebus coucang*). The local people said that the crab-eating macaques had intruded into this area within the ten years that preceded the study.

METHODS

The field study was conducted during three periods: from January to March 1985, from June 1985 to March 1986, and from July 1986 to February 1987. The study area of around 5 km^2 was divided by observation paths into a grid with sides of 100 m. Throughout the entire study period, the pigtails were traced by one or more tracker teams which included local assistants, and their ranging routes were mapped. The total visual and vocal contact time with the groups which ranged naturally amounted to 858 hr (309 encounters).

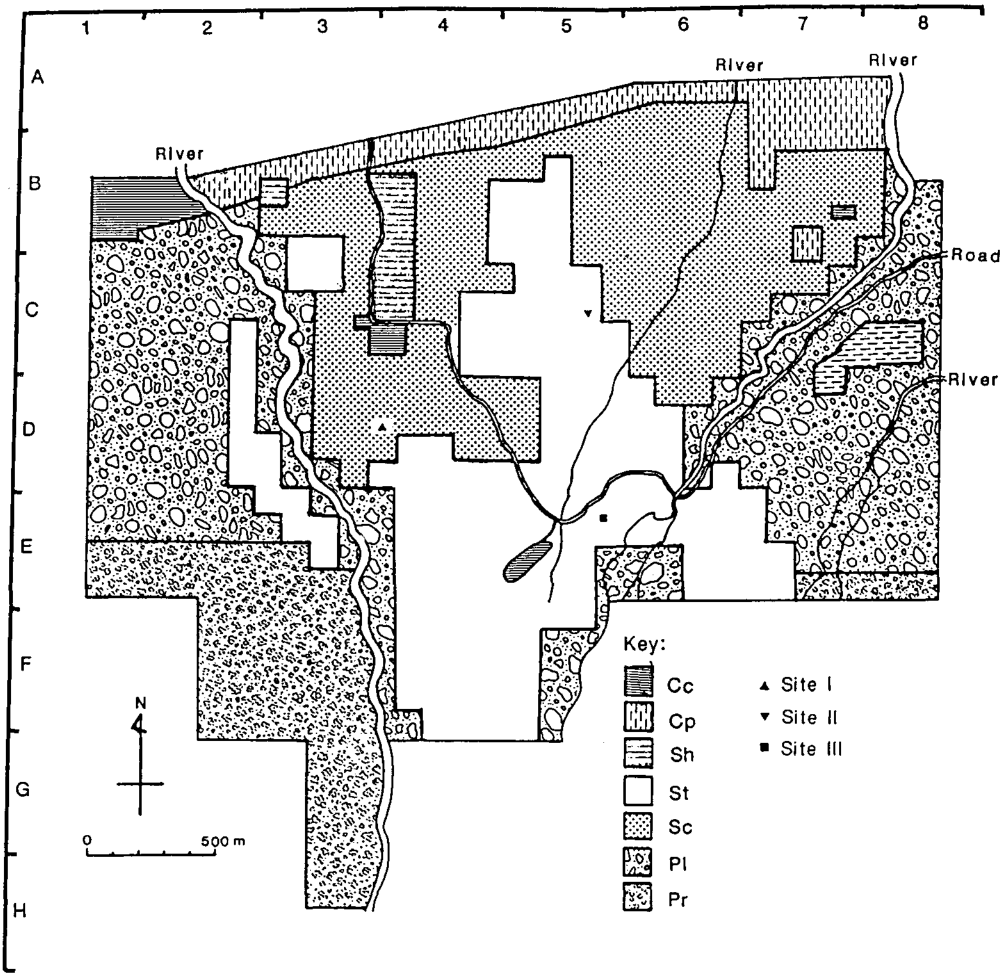

Fig. 3. Vegetation in the study area, based mainly on the vegetation in 270 systematically sampled plots (10×10 m^2). Cc: Cultivated area or open area; Cp: coffee (*Coffea* sp.) plantation; Sh: covered with tall (>2 m) herbs and shrubs; St: secondary forest recovering from evacuated tea (*Thea sinensis*) plantation, in which 10–85% of the trees (5 cm≦DBH) were tea; Sc: secondary forest recovering from heavy cutting, containing stands of trees with 5 cm≦DBH<50 cm; Pl: selectively logged primary forest, containing stands of some trees with DBH≧50 cm and some large stumps; Pr: primary forest, containing stands of some trees with DBH≧50 cm. DBH: Diameter at breast height. Sites I–III were the baiting sites. The positions of the vertical axis A–H and the horizontal axis 1–8 correspond to those of the same axis in Fig. 6.

From January 22 to March 2, 1986, and from July 17, 1986 to February 13, 1987, I provisioned and observed the animals at the baiting sites. Three baiting sites (Sites I, II, & III) were originally set up in the study area, but the last one was abandoned when the monkeys stopped visiting it after pitching of the blind. Each site consisted a square with sides of 20 m in a wood of Jambu Raden trees (*Melastoma* sp.), the fruit of which was one of the natural foods of the pigtails. The bait, 5–15 kg unshelled peanuts (*Arachis hypogaea*), was supplied on every occasion during which observations were made. At the beginning of provisioning, the bait was supplied continuously without any observation of the animals, for about a month. When I had confirmed that the animals visited the site regularly to eat the bait, I pitched a blind. After two or three days, when the animals had become accustomed to the blind, I waited in the blind for the animals and observed them through peepholes.

An attempt was made to identify and record all of the individuals that appeared at the sites. I employ the term "troop" to refer to a complete unit group and "group" to refer to any aggregate of animals where I failed to determine whether it was a subset of an entire troop or an entire troop itself (CROCKETT & WILSON, 1980). The troop as a unit group was recognized in terms of the stability of its membership and the social interactions between the groups. Three troops (Troops A, B, & C), two groups (Groups E & F), and ten solitary males were observed at the sites. An additional troop, Troop D, which was composed of about 40 animals, ranged in the western part of the study area. However, Troop D did not visit the baiting sites.

Groups E and F were recognized because they were composed of individuals not known to be part of Troops A, B, and C. However, since Groups E and F visited Site II just once, I was unable to assess whether they were actually troops or not. The age-sex composition of Group E was three adult males, two adolescent males, six adult females, nine juveniles, and three infants, while Group F was composed of one adult male, one adolescent male, three adult females, and one adolescent female (for definition of the age-sex classes, see below).

Table 1 shows the numbers of occasions on which observations were made, and the duration of the observations for each troop, group, and the solitary animals. Prior to the end of September 1986, the adolescents, the adults, and some juveniles of Troops A and B had been identified, and all adult males, some adolescent males and some adult females had been identified in Troop C. The dominance rank order of the individuals within each troop was determined on the basis of the outcome of dyadic agonistic interactions (OI, in prep.).

The age-sex classes were distinguished according to the body size and secondary sexual characteristics of the monkeys, mostly utilizing the criteria employed for Japanese macaques (YAMAGIWA, 1979). *Adult male*: estimated age of over 9 years old, with complete secondary sexual traits; a red-colored penis, and muscular especially around the shoulders; *Adolescent*

Table 1. Details of observations at the baiting sites.

Name of unit¹⁾	Site	No. of visits²⁾	Time (min)
Troop A	I	110	2322
Troop B	I	102	4534
Troop C	II	19	794
Group E	II	1	78
Group F	II	1	18
DO (sol.)³⁾	I	2	34
KR (sol.)³⁾	I	3	24
BK (sol.)	I	69	766
BT (sol.)	I	7	31
JR (sol.)	I	1	5
EX (sol.)	I	1	7
MY (sol.)	I	1	6
DS (sol.)	II	15	185
GD (sol.)	II	3	48
MK (sol.)	II	18	132
Total		353	8984

1) sol.: Solitary male; 2) number of visits by the social units to the sites. The author remained in the blinds for observations amounting to a total of 171 times at Site I, and 54 times at Site II; 3) joined Troop A on some occasions.

male: estimated age of 5–9 years old; suspension of the testicles; *Adult female*: estimated age of over 5 years old; periodic swelling of the sexual skin, parous, and nipples elongated by suckling; *Adolescent females*: estimated age of 3.5–6 years old; periodic swelling of the sexual skin, nulliparous; *Juvenile*: estimated age of 1–4.5 years old for males, and 1–3.5 years old for females and; Infant: less than 1 year old; blackish fur.

The names of the individuals are represented by two-letter codes. Codes with two capital letters represent the names of males, and codes with a capital letter and a small letter represent the names of females.

RESULTS

SIZE AND AGE-SEX COMPOSITION OF TROOPS

A multi-male, multi-female composition emerged as the configuration of the unit group (troop), through examinations of the stability of membership, and intergroup interactions, as outlined in the following sections (Table 2). The number of animals in the troops ranged from 49 to 81. The ratio of mature to immature animals (*adult and adolescent*: *juvenile and infant*) was 1:1.3 for Troop A, 1:1.2 for Troop B, and 1:1.3 for Troop C, respectively.

Although each troop contained three or four adult males, the sex ratio was biased by the presence of a larger number of females than males. The adult sex ratio (adolescent and adult sex ratio) in the troops was 1:7.3 (1:3.0) for Troop A, 1:4.7 (1:2.1) for Troop B, and 1:6.5 (1:3.5) for Troop C, respectively.

To identify the factors which lead to a departure from a balanced sex ratios of the troops, we need to examine the sex ratio of the population in this area. The sex ratio of the population was calculated from the total numbers of individuals from five years upwards that appeared at the baiting sites. This sex ratio was 1:1.6, and this figure implied the possibility that the number of females may have been greater than that of males in the population. However, since there could have been some solitary males who did not appear at the baiting sites, the true difference might be slighter.

The population density of this area (*number of individuals observed in the area/study area*) was approximately 53 individuals per km^2. In the upper part of the study area, the slopes became steeper and primary forest occupied a much larger proportion of the area. I penetrated up to 1,500 m a.s.l. on three occasions, but since I never found any pigtails on these expeditions, the density is thought probably to be very low in the upper part of the area.

INTEGRATION OF TROOPS AS FORAGING UNITS

Two types of troop, in terms of their integration, were recognized. There were troops which always appeared at the baiting site with an almost complete complement of members and appeared to forage as a tightly knit group even outside the baiting site (Troops A & B). The

Table 2. Sizes and age-sex composition of troops.

Troop name	Adult male	Adolescent male	Adult female	Adolescent female	Juvenile	Infant	Total
Troop A	3	5	22	2	27	15	74
Troop B	3	4	14	1	18	9	49
Troop C	4	4	26	2	34	11	81

other type of troop was one which appeared at the baiting site with a fluid membership within the troop and appeared to participate in frequent subgrouping (Troop C).

The group sizes of Troops A, B, and C were counted mainly at the baiting sites from February 1986 to February 1987 (Fig. 4). The group sizes of troops A and B were found to be stable. Excluding the number of infants, the size of the group comprising Troop A was concentrated at around the 50 level ($\bar{x}$ = 54, S.D. = 5.3, N = 12), while that of Troop B was concentrated at around the 30 level ($\bar{x}$ = 37, S.D. = 3.7, N = 12), and these values coincided more or less with the troop sizes from which the number of infants had been excluded: 59 for Troop A, and 40 for Troop B. By contrast, the group size of Troop C fluctuated from the 20 level to the 70 level ($\bar{x}$ = 51, S.D. = 16, N = 16).

Each individual who appeared as a member of a given troop never appeared with other troops, except for the case of one adolescent male, *DK*. The attendance rate for each individual in Troops A and B at the baiting site was calculated (Table 3). As the times of completion of identification for each individual differed, the periods during which the data were obtained for analysis differed according to sex: for males, since July 1986 (Troop A, N = 96; Troop B, N = 83); and for females, since October 1986 (Troop A, N = 61; Troop B, N = 66).

A difference between the sexes was recognized in the attendance rates. The rate for any of the females was almost 100%. *St* of Troop B had a rate of 78.8% because one of her legs had been damaged by a snare, and for a while, she was unable to keep up with the movements of the troop. In contrast to the case of the females, the attendance rates for the males differed according to the individuals in question. The individual monkeys could be grouped into three categories according to their rates of attendance: (1) those with attendance rates of more than 80%, who moved as stable troop members; (2) those with attendance rates of around

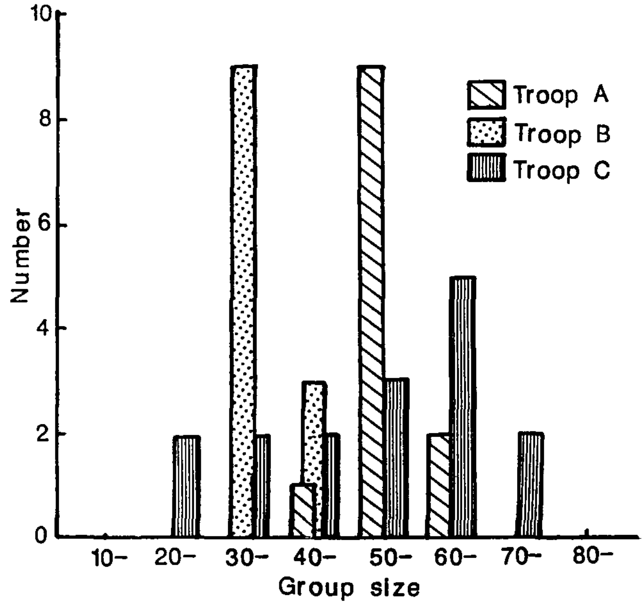

Fig. 4. Distribution of group sizes for Troops A, B, and C. The groups were counted when entering the baiting sites, when feeding at the sites, and when crossing the road (two occasions for Troop A). The number of infants was excluded from the quantification of the groups. The sample sizes were 12 for Troop A, 12 for Troop B, and 16 for Troop C.

Table 3. Attendance rate of each individual in each troop.

Troop A					Troop B				
NC1)	Age	*N*2)	*n*3)	A. rate4)	NC1)	Age	*N*2)	*n*3)	A. rate4)
NU	adult	96	92	95.8	*AM*	adult	83	82	98.8
NS	adult		89	92.7	*RS*	adult		81	97.6
NR	adult		93	96.9	*ID*	adult		76	91.6
DO	adult		21	21.9	*JN*	adolescent		82	98.8
KR	adult		6	6.3	*SR*	adolescent		83	100.0
KM	adolescent		62	64.6	*HG*	adolescent		83	100.0
IK	adolescent		91	94.8	*PT*	adolescent		80	96.4
KA	adolescent		85	88.5	*NP*	adolescent		1	1.2
AK	adolescent		66	68.8					
IN	adolescent		94	97.9					
MN	adolescent		8	8.3					
DK	adolescent		1	1.0	*DK*	adolescent		2	2.4
PR	adolescent		1	1.0					
Cw	adult	61	61	100.0	*St*	adult	66	52	78.8
Ef	adult		61	100.0	*Hn*	adult		65	98.5
Mr	adult		61	100.0	*Kg*	adolescent		64	97.0
Mi	adult		61	100.0	*Ks*	adult		63	95.5
Dn	adult		61	100.0	*Ab*	adult		65	98.5
Mo	adult		61	100.0	*Kn*	adult		66	100.0
Em	adult		61	100.0	*Tr*	adult		65	98.5
Mm	adult		61	100.0	*Yt*	adult		66	100.0
Up	adult		61	100.0	*Po*	adult		66	100.0
Uu	adult		61	100.0	*Na*	adult		65	98.5
Hr	adult		61	100.0	*Ni*	adult		66	100.0
Ww	adult		60	98.4	*Ng*	adult		64	97.0
Rt	adult		61	100.0	*Tk*	adult		66	100.0
Ii	adult		61	100.0	*Gi*	adult		64	97.0
La	adult		61	100.0	*Mg*	adult		66	100.0
Li	adult		61	100.0					
Pi	adult		60	98.4					
Me	adult		60	98.4					
Ma	adult		61	100.0					
Bt	adult		61	100.0					
Ys	adult		61	100.0					
Ae	adult		61	100.0					

1) Codes of individual names; the codes presented as double capitals are for males, and those presented as a capital and a small letter are for females. The individuals are arranged from top to bottom essentially according to their dominance rank order within the same sex class; 2) No. of observations of each troop; 3) No. of observation days for each individual; 4) attendance rate, which is given by $n/N \times 100$.

60%, who usually moved as troop members but often separated from the troop, i.e., loosely attached troop individuals; and (3) those with attendance rates of less than 25%, who joined the troop temporarily. The former two categories define troop individuals, and the last category defines temporary troop individuals. In the previous section, only the troop individuals were included in the counting of the sizes and compositions of the troops. Two adolescent males (*KM* & *AK*) in Troop A belonged to the class of loosely attached troop individuals. The temporary troop individuals included two young adult males (*DO* & *KR* in Troop A) and four adolescent males (*MN* & *PR* in Troop A, *NP* in Troop B, and *DK* in both Troops A and B). These individuals were comparatively young and low-ranking.

Thus, most of the members foraged together with the exception of the temporary troop individuals in Troops A and B. In particular, the stable troop individuals were scarcely ever absent from the troops. *ID*, the third-ranking adult male of Troop B, was temporarily absent from Troop B from January 29, 1987 to February 2, 1987, and appeared again in Troop B

Table 4. Sizes and composition of groups of Troop C in 1986.

Date	Age-sex class Adult male (Individuals)[1]	Adolescent male	Adult female	Adolescent female	Juvenile	Infant	Total
Aug. 18	4 (*KK*, *HS*, *MS*, —, *HT*)	3	7	1	19	1	35
Aug. 29	3 (*KK*, *HS*, *MS*, —, —)	2	17	1	34	3	60
Aug. 30	3 (*KK*, *HS*, *MS*, —, —)	1	10		19	2	35
Sept. 23	3 (*KK*, *HS*, *MS*, —, —)	3	12		28	4	50
Sept. 25	3 (*KK*, *HS*, *MS*, —, —)	3	14	1	25	4	50
Oct. 3	1 (—, —, *MS*, —, —)	3	8	0	12	2	26
Oct. 10	4 (*KK*, *HS*, *MS*, *IM*, —)	1	23	0	34	2	64
Oct. 17	4 (*KK*, *HS*, *MS*, *IM*, —)	2	14	0	33	2	55
Oct. 24	3 (*KK*, *HS*, *MS*, —, —)	1	7	0	10	0	21
Nov. 6	4 (*KK*, *HS*, *MS*, *IM*, —)	2	26	0	40	5	77
Nov. 7	4 (*KK*, *HS*, *MS*, *IM*, —)	2	21	0	26	3	56
Nov. 12	4 (*KK*, *HS*, *MS*, *IM*, —)	4	18	1	37	3	67
Nov. 13	4 (*KK*, *HS*, *MS*, *IM*, —)	3	14	4	37	9	71
Nov. 15	4 (*KK*. *HS*, *MS*, *IM*, —)	4	20	2	34	10	74
Dec. 2	4 (*KK*, *HS*, *MS*, *IM*, —)	4	26	2	34	11	81
Dec. 13	2 (*KK*, *HS*, —, —, —)	4	17	3	34	11	71

1) The codes in parentheses represent the code names of adult males who were present in the groups; —: absence of the individuals.

on February 9, 1987. On one occasion, in Troop B, two adult males (*RS* & *ID*), three adult females (*St*, *Hn*, & *Ks*), one adolescent female (*Kn*), some juveniles, and an infant disappeared simultaneously (February 1, 1987). They may have temporarily split from the other members of the troop.

Although the attendance rates for Troop C could not be calculated, it is quite clear that the group size of this troop varied enormously from 21 to 81 (Table 4), and these variations indicated that the members of Troop C repeatedly formed subgroups. Five adult males (*KK*, *HS*, *MS*, *IM*, & *HT*) observed in this troop were identified since the first observation. The attendance rates for these five males with the females of Troop C were: for *KK*, 89.5%; *HS*, 89.5%; *IM*, 52.6%; *MS*, 89.5%; and *HT*, 5.2%. While *KK*, *HS*, and *MS* always visited the site together (16 out of 19 visits of Troop C), only *MS* was observed in the group when 26 individuals were counted at the baiting site on October 3, 1986. *IM* was frequently absent from the groups in which *KK*, *HS*, and *MS* were present (6 out of 19 visits of Troop C), and on such occasions the group sizes were smaller (Mann-Whitney $U = 2$, $N_1 = 8$, $N_2 = 6$, $p < 0.01$, one-tailed).

While the trackers followed the natural foraging of Troops A, B, and D, they did not notice any signs of subgrouping (during 202 hr of contact time after 57 encounters from August 1986 to February 1987). However, when Troop C was followed, the groups sometimes split and moved in different directions (nine cases in 298 hr of contact time, after 61 encounters, from August 1986 to February 1987). However, the detailed compositions of the groups and the ways in which they moved and fused again were uncertain.

MALE IMMIGRATION INTO AND EMIGRATION FROM THE TROOPS

Immigration into and emigration from the troops were restricted to males: such behavior by females was never observed. The temporary troop males might represent males who joined the troop for a short time. Although the temporary troop males were tolerated by the

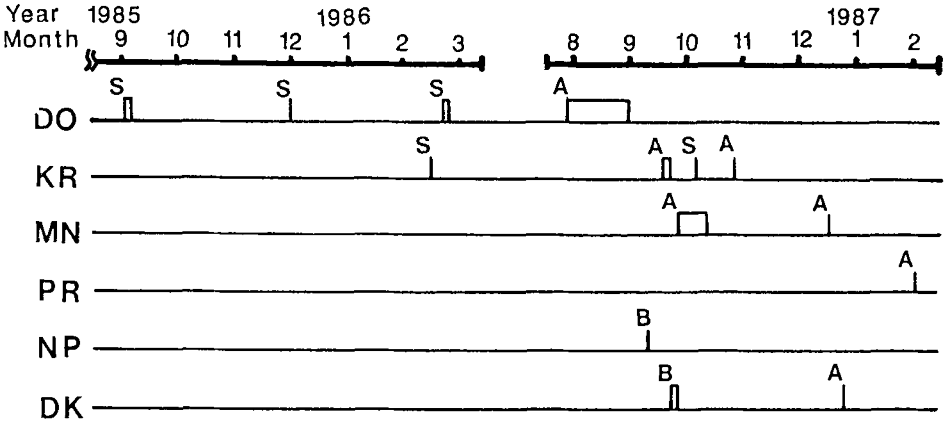

Fig. 5. Observations of temporary troop males. Vertical lines and squares indicate the periods when each male was observed. "S" indicates that the male was observed as a solitary; "A", as a member of Troop A; and "B", as a member of Troop B.

troop individuals, and in particular by the troop males, solitary males were never tolerated.

As temporary troop males, two adult males (*DO* and *KR*) and three adolescent males (*MN*, *DK*, and *PR*) appeared in Troop A; an adolescent male (*NP*) appeared in Troop B; and an adolescent male (*DK*) appeared in both Troops A and B (Fig. 5). Only *DO* and *KR* were observed while leading a solitary life before or after they appeared in Troop A. In the case of Troop C, it was difficult to identify immigrants and emigrants because of the frequent subgrouping.

Males appeared to leave the troops when they were more than 4 years old, because the sex ratio for individuals of 4 years old and under in Troop B, in which the sex of all individuals was known, was 13:14. This value implied that males of this age class had not yet emigrated from the troop. Furthermore, the estimated age of the solitary males ranged from 7 to 16 years ($N = 8$) and that of the temporary troop males ranged from 5 to 12 years ($N = 6$). It is worthy of note that individuals of 5 and 6 years of age were observed not as solitary males but only as temporary troop males ($N = 4$).

INTERACTIONS BETWEEN TROOPS AND SOLITARY MALES

The interactions between the troops and solitary males were generally antagonistic. In particular, the dominant troop males were antagonistic to the solitaries. However, estrous females and peripheral individuals, such as young males, sometimes showed a permissive attitude towards the solitaries who frequently approached their troop. The solitary males occasionally copulated with estrous females and interacted non-agonistically with the peripheral males of the troop.

BK, an adult male, visited Site I (69 cases). When *BK* fed at the site, it happened occasionally that either Troop A (9 cases) or Troop B (14 cases) appeared at the site. In all of these cases, *BK* retreated from the site immediately without any direct confrontation. On two occasions, *BK* shook a tree without articulating any sounds against the troop individuals. The alpha or the beta males of Troop A and Troop B then rushed in that direction, and agonistic voices [go·go·go] and the sound of violently swaying branches were heard. These males may have attacked *BK*. *BK* was observed to copulate with *Kn*, an estrous adult female of Troop B, on one occasion. After Troop B left to go southwards, *Kn* approached *BK*, who was outside of the site on the north side and copulated with him.

At Site II, several encounters between Troop C and solitary adult males (*GD* and *DS*) occurred. When the troop males came to the site with the troop individuals, the solitaries retreated. However, *GD* appeared at the site with an estrous female of Troop C, and copulated with her on one occasion, and *DS* appeared at the site with an estrous females on two occasions. Consortship between solitary males and troop females was temporary, and the females returned to the troop afterwards.

INTERACTIONS AMONG SOLITARY MALES

Sometimes more than one solitary male appeared at a site simultaneously (seven cases). Their attitudes could be categorized into three patterns, according to the degree of proximity, which appeared to reflect the degree of acquaintanceship or familiarity between them. First, an individual *B* who had fed at the site left the site as soon as a dominant individual *A* approached him, and then *A* started to feed alone (two cases). Second, three individuals were seen around the site, but none of the individuals entered the site, as if each was nervous about the other (one case). Third, two individuals fed simultaneously, but they did not come close to each other while feeding (four cases). A kind of greeting behavior was carried out, such as puckering (BERNSTEIN, 1966, 1967) and non-copulatory mounting (two cases). The directions in which they left, and their attitudes to each other indicated they had just happened to meet at the site.

INTERACTIONS BETWEEN TROOPS AND THE HOME RANGES

Troops A and B both visited Site I, and often encountered each other (21 cases). Usually, Troop A approached Troop B when the latter troop was feeding at the site, and Troop B retreated quickly, without aggressive interactions (10 cases) or with aggressive interactions such as threats and chasing (11 cases). These observations imply that Troop A was dominant over Troop B (CHENEY, 1981). As soon as Troop B retreated, Troop A usually began to feed. However, in two cases, Troop A pursued Troop B when the leftover amount of bait was small. Antagonistic encounters occurred before provisioning, also. On July 26, 1985, the group which I was tracking encountered another group which was being followed by another tracking team. After a brief interval, the groups crossed the road one after another, separated again, and moved off in different directions. Before and after the two groups crossed the road, agonistic voices and tree-shaking were frequently heard.

Attacks were always started by individuals from Troop A, and they ended with the retreat of Troop B. The attackers included individuals of any dominance status, if juveniles and infants were excluded from consideration (Table 5). The alpha and beta males participated most frequently in the attacks. Females participated in 100% (ten occasions) of aggressive interactions, while males participated in 80% (eight occasions) of the interactions, and in one case the participants were unknown. The targets of the attacks were not obvious. The alpha male and the beta male of Troop B always retreated promptly, but in one case they chased the members of Troop A: when Troop B was feeding at the site, the beta male and two females (3rd-ranking and 14th-ranking), who preceded the main body of Troop A, intruded onto the site, and the alpha male and beta male of Troop B chased them. However, as soon as the main body of Troop A approached, Troop B retreated.

Table 5. Number of aggressive encounters in which each male or female participated as an aggressor.

Male			Female		
Attacker	Rank[1]	N[2]	Attacker	Rank[1]	N[2]
Troop A:					
NU	1	4	*Mr*	3	1
NS	2	4	*Mi*	4	1
NR	3	3	*Li*	16	1
KR	6	1	*Pi*	17	1
AdlU[3]	?	1	*Ad*	22	2
			AdU[4]	?	1
Troop B:					
AM	1	1			
RS	2	1			

1) Dominance rank order within the same sex class; 2) No. of aggressive encounters in which an individual participated as an aggressor. The total number of aggressive encounters was 11; 3) unidentified adolescent; 4) unidentified adult.

Some individuals of the two troops fed together on two occasions. In one case, when females (middle- and low-ranking: 7th, 8th, 10th, and 14th) and some juveniles of Troop B were feeding after the main body of the troop had left the site, the third-ranking male of Troop A joined them. The females from Troop B did not come close to him and the male did not chase the females. Finally, as soon as the main body of Troop A arrived, the females from Troop B retreated. In another case, when females (low-ranking: 11th, 12th, 14th, and 15th), some juveniles, and the 3rd-ranking male of Troop B were feeding, a middle-ranking (14th-ranking) female and an adolescent male (5th-ranking) from Troop A joined them. The two members of Troop A stayed together and avoided the individuals from Troop B, but when the main body of Troop A finally arrived, all of the individuals from Troop B retreated.

The home ranges were determined by summing up the enclosed quadrats (which were delineated by the observation paths at intervals of 100 m) at and within the outermost traces of movement of the troops (Fig. 6). Troops A and B appeared only at Site I, and Troop C appeared at Site II (cf. Table 1). Troops A and C utilized the coffee plantation on the northern side of the study area, but the extent to which they intruded into that area was uncertain. Therefore, the home range of Troop A was greater than 140 ha, and that of Troop C was greater than 153 ha. The western part of the home range of Troop D was unknown. Only the range of Troop B was completely enclosed within the study area and was accurately estimated (127 ha). The known home ranges of each of the troops overlapped considerably: 87% for Troop A, 79% for Troop B, and 99% for Troop C. The extent of overlap of the home ranges between Troops A and B (*area of overlapping part of the home ranges between Troop A and Troop B* ×100/*area which the home ranges of Troops A and B occupied*) was less than 39%; for that between Troops A and C, it was less than 13.3%; and for that between Troops B and C, it was less than 3.2%.

DISCUSSION

TROOP SIZE AND SEX RATIO

The troop sizes of pig-tailed macaques range from 6 to 81 individuals ($\bar{x} = 36$, S.D. $= 22$, $N = 17$; MACCLURE, 1964; BERNSTEIN, 1967; RIJKSEN, 1978; RODMAN, 1979; CROCKETT &

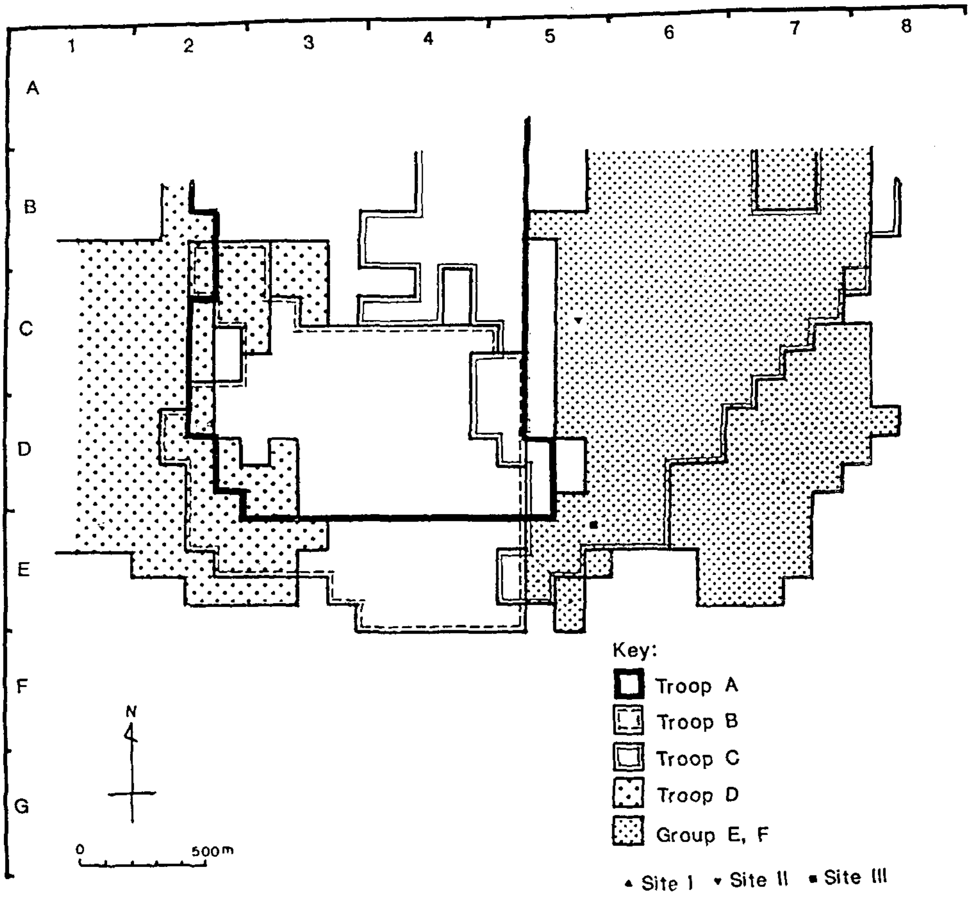

Fig. 6. Home ranges of the pigtail troops.

Wilson, 1980; MacKinnon & MacKinnon, 1980; Caldecott, 1986; this study). The troop sizes at Lima Belas (Bernstein, 1967; Caldecott, 1986; the "group" of Caldecott should coincide with our definition of a troop), and at Mt. Kerinci (this study) are the largest among those reported, ranging from 47 to 81. If the data from these two sites are excluded, the mean troop size becomes 19 (range, 6–35, $N = 9$). The most conspicuous difference in habitat between these two sites and the others is that at the former sites, secondary forest occupies a large fraction of the area (Caldecott, 1986). The larger group size might be explicable in terms of such a forest structure. Secondary forest at a certain stage of its succession has a rather higher plant productivity than primary forest, and includes patches where the same one or a few species grow together (Whitmore, 1984). Such patches provide large feeding sites for monkeys. Given that intratroop competition for food can inhibit the formation of large troops (van Schaik & van Hooff, 1983), the large food patches in such secondary forest can permit and sustain the existence of large troops. Furthermore, in past studies (e.g., MacClure, 1964; Crockett & Wilson, 1980), the possibility exists that only part of the troops was counted and the troops may have been estimated to be of smaller size than they actually were, because the observers did not allocate sufficient time to recognize the whole troops owing to the nature of their study.

The mean adult sex ratio in the troop was 1 :6.3; that is, markedly biased towards females, in the same way as in the case of the Malayan pigtails (1:8) which CALDECOTT (1986) studied. There is some possibility that hunting pressure might depress the male population, although such an effect may not be so significant since the approximate adolescent and adult sex ratio of the population (1:1.6) indicated only a comparatively small bias. In south-east Asia, pigtails are used to pick coconuts at the heights of the trees where it is dangerous for men to approach. The Minankabau tribe, the main dwellers of West Sumatra, capture many pigtails for this purpose. Although no monkeys were hunted during the study period, some abandoned traps were found in the study area.

A more important factor in the distortion from a 1:1 sex ratio among the matures in the troop could be immigration into and emigration from the troop by males. Solitary males have been observed at many study sites (BERNSTEIN, 1967; RIJKSEN, 1978; CROCKETT & WILSON, 1980; CALDECOTT, 1986; this study). The mobility of the males suggests that the unit group (troop) should be matrilineal.

There is a clear difference in the adult and adolescent sex ratios of the troop between Japanese macaques and pig-tailed macaques. On the western coast of Yakushima Island, the population of Japanese macaques reveals similar features to that of the pig-tailed macaques on Mt. Kerinci: a high troop density [Yakushima, 1 troop/km^2 (IWANO, 1983); Mt. Kerinci, 0.94 troops/km^2], a high individual density [Yakushima, 33 individuals/km^2 (MARUHASHI, 1982); Mt. Kerinci, 52.8 individuals/km^2], and no physical barriers to prevent intertroop transfer by males (TAKASAKI & MASUI, 1984). However, the adult and adolescent sex ratio in the Yakushima troop was nearly 1:1 (MARUHASHI, 1982; FURUICHI, 1985), while that of the Mt. Kerinci troop was 1:2.9, a much higher value than the estimated sex ratio of the whole population on Mt. Kerinci (1:1.6). The difference in sex ratio within the troop, between Japanese and pig-tailed macaques, might reflect a difference in the troop individuals' tolerance of solitary males between the two species. I suggest that this difference may be ascribable to the difference in mating systems between the two species. Since the Japanese macaque is a seasonal breeder where the females tend to become estrous simultaneously and the pig-tailed macaque is a year-round breeder where the females tend to become estrous separately, the available females as mates at any given time will be fewer for pigtail males than for Japanese macaque males, and the pigtail males will tend to be more competitive for females. Thus, fewer males can be expected to coexist with a given number of females in the pigtail troop than in the Japanese macaque troop (OI, in prep.).

Just as male Japanese macaques leave their natal troops at 3 to 5 years of age and transfer to other troops or become solitaries (NISHIDA, 1966; SUGIYAMA, 1976), male pigtails leave their natal troops at around 5 years of age. The males of 5–6 years of age lived as temporary troop individuals, not yet as complete solitaries. Since such newly solitarized young males might not be experienced in solitary life and might be vulnerable to predation, they have no option of living a completely solitary life. After repeating temporary stays in some troops, they may become complete solitaries at an older age. In the present study, the solitaries, *BK*, *DS*, and *MK*, appeared at the same baiting site for periods of one to seven months. Like them, some solitary males among the pigtails remain for long periods in one fixed area (RIJKSEN, 1978). Although some solitaries happened to meet at the baiting site, they did not organize themselves into male groups. However, ROBERTSON (1986) did observe cases of a "all-male groups, composed of two or three sub-adult males and/or large juvenile males." Such a group might correspond to the male group of Japanese macaques which is organized by peripheralized males or new immigrant males (YAMADA, 1966; NORIKOSHI & KOYAMA, 1975).

SUBGROUPING

The attendance rates of females in Troops A and B were almost 100%, and the females were the most stable members of the troops, while the attendance rates of males were variable. If temporary troop males were excluded, Troops A and B maintained their integrity as single ranging units through the females, their offspring, and higher-ranking males. In contrast, Troop C frequently formed subgroups; that is, females, who were the most stable members of Troops A and B, temporarily split from the main troop. Among four top-ranking adult males (*KK*, *HS*, *MS*, and *IM*) of Troop C, *KK*, *HS*, and *MS* almost always visited the baiting site with females, while *IM* was frequently absent. Even when all of these four adult males, including *IM*, appeared together (October 17, November 12, and November 13, 1986), the number of animals, especially the number of adult females in the group, was smaller than the possible total, indicating the occurrence of subgrouping. These observations imply that *IM* and the three other adult males did not play a positive role in the formation of subgroups as harem-type units. Rather, they just followed the female subgroups, as has been observed during the fission process in the case of Japanese macaques (OI, 1988). If the harem-type units, which are organized by a special bond between a male and some females in the group (CALDECOTT, 1986; ROBERTSON, 1986), represented the units of subgrouping observed in this study. then the absence and attendance of the four adult males (*KK*, *HS*, *MS*, and *IM*) should have been linked with the number of attending females in Troop C. However, since the observed results did not coincide with this assumption, the hypothesis of the harem-type unit can be rejected for the present study population. In pigtails, the multi-male troop might be essentially a stable foraging and reproductive unit. This conclusion is also supported by the finding that the mating partners of each dominant male include the females from the whole estimated kin groups: there was no fixed mating bond between a male and some females (OI, in prep.).

Previous workers have stressed subgrouping as the grouping tendency in pigtail macaques (RIJKSEN, 1978; CROCKETT & WILSON, 1980; CALDECOTT, 1986; ROBERTSON, 1986). In the present study. the tendency towards formation of subgroups varied among the troops: Troops A and B did not form subgroups, while Troop C formed them frequently. Such intertroop variation indicates that subgrouping might tend to occur under certain sociological or demographic conditions, as observed in the process of fission of the Japanese macaque troop (MARUHASHI, 1982). The data strongly suggest that Troop C was in the process of social change: the dominance relationship between two top-ranking males (*KK* & *HS*) underwent a reverse, while the dominance rank order among the top-ranking males of Troops A and B was stable and strictly linear (OI, in prep.).

Ecological factors, such as intratroop competition for food, might combine with sociological and demographic factors to cause subgrouping (VAN SCHAIK & VAN HOOFF, 1983). Troops A and B significantly overlapped in terms of their home ranges, but their home ranges overlapped only slightly with that of Troop C. Some significant environmental differences might exist between the home ranges of Troop A and Troop B, and that of Troop C, which the present study did not detect. To examine this possibility, detailed studies of the food environment and actual conditions of competition for food are needed.

INTERTROOP RELATIONSHIPS

Since CALDECOTT (1986) described that pigtails tended to spend most of their time in a multi-male bisexual "group," his term "group" possibly coincides with the troop as used in the present study. He also suggested that "super-groups" emerge as a result of the temporary fusion of "groups." However, the present study indicated that pigtail troops were antagonistic to each other and that the subordinate troop foraged while avoiding the dominant troop. Troop fusion, based on non-antagonistic relationships between troops, was never observed.

In the interactions between troops, the higher-ranking individuals participated actively. The alpha and beta males, in particular, showed an evident antagonistic attitude towards non-troop individuals, including solitaries. Furthermore, females, from lower- to higher-ranking members of Troop A, were also involved in such antagonistic interactions. However, middle- and low-ranking females of Troop B occasionally happened to feed together with the third-ranking male, middle-ranking females, and adolescent males of Troop A. Their attitude might be said to have been opportunistic. However, the configuration of the troop was rigidly maintained by some high-ranking individuals who discriminated between the members of their own troop and those of other troops.

BERNSTEIN (1967) reported that the home ranges of two troops overlapped to some degree, and that their encounters were peaceful. The "super-group" of CALDECOTT (1986) and the "mixed-band" of ROBERTSON (1986) might encompass groups which were observed during peaceful encounters between troops. The antagonistic relationships observed in the present study thus imply a variability of intertroop relationships in this species. Relationships between troops have been suggested to fluctuate according to the ecological situation, e.g., density of individuals (YAMAGIWA, 1987), history of establishment of the troops, history of interactions between troops, and history of exchanges of members among troops (CHENEY, 1981). We do not need to view the changeable nature and patterns of the intertroop relationships as the super-structure of the society.

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